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1160 W. Orange Grove Ave., Arcadia, California 91006, U.S.A.

TOWARD A THEORY OF BUTTERFLY MIGRATION

OAKLEY SHIELDS
Department of Entomology
University of California, Davis, California 95616

INTRODUCTION

It is difficult to know what observations are important or critical in explaining why and how butterflies migrate, but since so many have been made, some of these are bound to be of significance. Regrettably, there is a nearly total lack of experimental work. A good working model is sorely needed; the lack of this has no doubt severely hampered progress in this field. This report is my attempt to extract a working hypothesis from the morass of published data.

Butterfly migrations can reach spectacular proportions. In 1926 in East Africa about 36 million *Belenois mesentina* crossed each mile of front per day, and in 1924 in southern California about 3 billion *Vanessa cardui* crossed a 40-mile front (Williams, 1949)! On the other hand, flights may be "so thin that each butterfly may be hundreds of yards from its nearest companion," out of sight of each other (Williams, 1949).

The two questions which most commonly occur are: (1) Why do they migrate?, and (2) What determines the direction of migration? (Abbott, 1950).

Various authors have offered their definition of butterfly migration. (Poulton, 1902, says that *emigration* is a better term than migration, for masses of insects moving out of an overcrowded area, but the term does not specify that a undirectional flight also occurs.) Wiltshire (1946) says as a general rule, migrant Lepidoptera do not perform a diapause. "A species can be considered a migrant if it fulfills most or all of the following provisions:—(1) it has been observed performing a mass movement; (2) it has been taken, or seen on the wing, at sea; (3) it shows no geographical variation over a wide and diverse area; (4) both sexes occur occasionally, or sporadically, far from where it is known to breed and reside." "A migration is recognized when the butterflies, whether few or many, are all at the same time flying in the same direction, as if guided by a compass" (Abbott, 1951). Williams (1957) says that insect migration refers "to movements of animals in a direction and for a distance over which they have control, and which result in a temporary or permanent change of habitat." "Migration is a persistent, straightened-out movement with some internal inhibition of the responses that will eventually arrest it" (Kennedy, 1961). Johnson (1960) says that insect migration is so variable that definitions based on what is or is not migration or what is active migration and passive dispersal become arbitrary and unsatisfactory when applied to all migratory insects.

EXAMPLES

Details of five species of migrants are presented below which are well-known in the literature, in hopes of revealing underlying causes.

VANESSA CARDUI

Williams (1925) says that *V. cardui* in Europe in the late spring fly mostly NW. These flights come from North Africa and Asia Minor, although not from the countries immediately surrounding the Mediterranean (probably from the deserts to the south). "The movement appears to continue for many weeks or even months at irregular intervals." He says there is *no* evidence of a return flight in this region in autumn. It cannot overwinter in the north in any stage. "So far as we can see, all those butterflies which fly to the north of the area in which they can breed throughout the year are lost completely to the species, as either they or their offspring perish during the winter." Migrant individuals have large fat body reserves and undeveloped internal sex organs.

Abbott (1950) records that 1924 was a great migration year for *V. cardui* in southern California, while in 1925 only 2 were seen the entire spring. 1926 was another migration year, though not in such large numbers as 1924. (Thus perhaps 1925 was a population crash.) "To maintain their straight path of migration, butterflies regularly rose over obstacles such as hedges and trees, even tall eucalyptus trees and three story buildings, yet they consistently kept within a few feet of the ground otherwise." The beginning of the daily flight was noted at 6:50 am on April 25, 1941, when 6 *V. cardui* which apparently had been "sleeping" on the lawn flew up, circled around more or less, and flew off to the northwest. (Similarly, migrant V. *cardui* I released in a room lighted by a ceiling light flew up to the light in a spiral flight, at night.) Abbott (1951) notes that in 1941 there were three waves: March 9-March 28, April 4-7, and April 15-22. In 1945 waves occurred on March 19-21, March 24-25, and March 27-29. "The same territory is covered in every migration, the extent varying with the total numbers." Flights are from February to April, averaging just under 2 months in extent. Migrations occur during years of vegetation abundance, though significantly not every "wildflower year" is a migration year. Southern California migration years were 1924, 1926, 1941, 1945, 1949. Tilden (1962) noted V. *cardui* moving NNE on May 18-19, 1958, in Oregon, and on May 20-21, moving SSW, perhaps due to meeting a cold front. He saw one V. *cardui* migration in light to heavy rain, and rather cold, though he thinks it unlikely the flight was initiated in the rain. Sampling of 2 flights by Thorne and Sette, and Tilden, yielded a 50-50 sex ratio. Tilden thinks V. *cardui* must reproduce along the line of flight.

On April 15-20, 1973, I encountered V. *cardui* migrating NNW (even against a wind) in vast numbers on the Eastern Mojave Desert, E of Ludlow 20-40 mi., by the thousands. The desert was carpeted with wildflowers. Desert blooms hit by the larvae included *Amsinkia, Lupinus, Salvia, Phacelia campanularia,* every Boraginaceae, and even 2 larvae on a crucifer. V. *cardui* was noted migrating and feeding in the pm and avidly feeding in the early am on white flowers in washes.

ASCIA MONUSTE

Hayward (1953) saw a migration of A. *monuste* in Argentina during the spring and summer of 1951-52. "On fine mornings the overnight ground population began to move with the first sign of daylight," seeking flowers and puddles. "Although the butterflies sometimes commenced their migratory flight directly from the flowers on which they were feeding, it was more usual for them to circle and drift upwards till they had attained certain height and there assemble before moving off." The migrations flew in various directions: 9 am = SSE then veering E; 11:30 = N (WSW wind). On December 3rd there was a massive migration that began to lessen at c. 3000′, with individuals seen by airplane pilots as high as 5000′! On December 7th at 9:15 am one flight at ground level was going E, while a high-flying swarm that was earlier going E was flying N! On January 7th the flight continued until darkness. On January 14, there was heavy overcast and no migration was observed. In one migration on October 28th, 300 specimens were taken at light on a moonless night. Females were observed laying eggs during one flight. "*Ascia monuste* on migration flies close to the ground when the wind is adverse and high when the wind is favorable. There is a tendency to fly low on cloudy days and higher in bright sunshine. The migratory swarms may reach an altitude of over 3000 ft., and mountain ranges of up to at least 5000 ft. in height do not cause the migrants to deviate from their course."

Nielsen & Nielsen (1950) report a migration of *A. monuste* at Fort Pierce, Florida, was at a maximum on April 15, and the maximum of the next outbreak was May 20, some 36 days later. They observed that a mass outbreak was necessary for a migration ("a simultaneous hatching of a whole population within a few days"). *A. monuste* migrates "*en masse* while there seems still to be ample food on which they could continue to breed in the habitat" (Johnson, 1969, p. 224).

URANIA MOTHS

Smith (1972) notes of *Urania* moths in the Neotropics, that, "Aside from the periods of population explosion and migration, the distribution of *Urania* moths over the vast area is rather localized," in low densities. "The migration is to the south and east in the autumn and westward and northward in the spring." Movement is basically east-west. The eastward movements (July-October) involve far more individuals than do the westward ones. "The most frequent interval between large flights appears to be 8 years, but there are numerous exceptions." In general there is no "return spring flight" in years following a large eastward movement in the autumn. Migrants fly all day long. Larvae eat the vine *Omphalea* (Euphorbiaceae). Some flight had many gravid females, others did not. In 1969, in the second and third weeks the frequency of gravid females increased. Copulation was rarely observed; no oviposition was observed during a flight. Release from selection pressure of predators and parasites combined with food abundance "must be responsible for the really major population explosions that have occurred." Generally when an eruption of *Urania fulgens* occurred in Central America, a simultaneous eruption occurred in *U. leilus* in South America.

DANAUS PLEXIPPUS

Tilden (1962) says that the monarch has a true migration, involving "a going out and a return," i.e. a cyclic movement. The migrants, however, do not fly in mass (Heape, 1931, p. 151). Migratory flights of monarchs end in aggregations for hibernation and thus differ from other migrant species where the flights lead to dispersal. In autumn, monarchs migrate south in the U.S. (Canada and northern U.S.), to southern California, Florida, Mexico, and hibernate gregariously in trees. They breed and migrate (disperse) north the following spring. Their foodplants grow in exposed and often semi-arid areas. Adults depart from the cold. To survive *in situ* as adult diapause in winter would be fatal. There are one to three generations in the north before next autumn. Flights are up to 1500 miles (tagged specimens). Urquhart (1960, p. 296) notes that "recovery lines" for tagged monarchs in eastern U.S. indicate a general SW flight in the fall. Spring migration records in California for tagged monarchs show a general NE or NNE trend (fig. 79, p. 320). Monarchs do seem to be affected by landmarks, water bodies, etc. in their migration flights.

Funk (1968) found *D. plexippus* in December at Yuma, Arizona, as ova, larvae, pupae, and adults. The implication is that a return flight might be from this new brood rather than from overwintering adults. (Marked specimens could not be recaptured in the area.)

Beall (1948) says that *D. plexippus* "freshly emerged in the autumn in Ontario start with a considerable fat reserve, some 30 per cent of the lean weight." Young migrants add even more; they have fat as high as 125% of lean weight. Migrants taken in New Orleans, presumably from a long journey, have fat only 2% of lean.

NYMPHALIS CALIFORNICA

Yothers (1913) reported that in 1912, *N. californica* larvae at a number of places in Washington, Idaho, and British Columbia were "by the millions," defoliating *Ceanothus velutinus*. At Clayton, Washington, the larvae had eaten all the leaves, and the branches were entirely bare except for the millions of larvae. On July 7, 1912, he found millions of larvae on Moscow Mt., Idaho. Then on July 13th, all the larvae and pupae were gone from the place of infestation. "The caterpillars had evidently not migrated, for all around as far as I could see the *Ceanothus* had not been touched. Even had the caterpillars migrated that would not explain the absence of the chrysalids. I think that the total disappearance of these caterpillars and chrysalids was no doubt due to birds."

On May 11, 1973, in Del Puerto Canyon, 22-23 rd. mi. W of Patterson, Stanislaus Co., Calif., I noted *N. californica* larvae all over most of the *Ceanothus integerrimus* bushes, stripping some bare, although some bushes were untouched (all stages of instars above ca. second or third). (Adult hibernants were fairly common there on March 11, 1973.)

William Neeley (pers. comm.) saw "millions" of *N. californica* one day during the first week of August, 1962, on the summit and sides of Triple Divide Peak, Yosemite, California, flying east from the SW San Joaquin drainage in a band ¾-1 mile, 1½-30′ in height, from noon to three pm; some were landing.

EXTRA SPECIES JOINING MIGRATION

One puzzling aspect of butterfly migrations, especially those in the tropics, has been the accompaniment of many species in the migration. For example, Welling (1959) notes one migration consisting "of just about everything imaginable," flying from N to S in the Yucatan Peninsula, especially *Anteos clorinde* and *A. maerula*, with *Eunica tatila* and *E. monima*, made up the bulk of the migration. Also *Papilio* sp., *Heliconius charitonius*, *Eurema* species, many *Libytheana carinenta*, *Danaus* sp., a few blues, *Phoebus*. He mentions (1964) *Eunica monima*, *Agraulis vanillae*, "and a few other odds and ends" accompanying a large migration of *Kricogonia castalia lyside* in Yucatan. Such observations appear to be explained by the following observation recorded by Poulton (1929, 1930): Mr. F. Muir observed "the sweeping up of the non-migrating butterflies on a Papuan island when a migratory flight from another island passed over it. In this instance, in which more than a single species was involved, it is evident that the social stimulus, and this alone, availed to compel the non-migrating butterflies to become migrants—with such success indeed that the island was comparatively depleted of these species after the migratory stream had passed."

MAJOR SPECIES OF MIGRANTS

The following species from Williams (1930) appear to be frequent, conspicuous migrants: *Catopsilia florella* (Africa), *C. sennae* (Americas), *C. statira* (South America), *C. pyranthe* (India, Ceylon), *C. pomona* (Ceylon, India, Java), *C. crocale* (Ceylon, India), *Belenois severina* (Africa), *B. mesentina* (Africa, India), *B. java teutonia* (Australia), *Appias albina* (Ceylon, India), *A. paulina* (Ceylon), *Ascia monuste* (Americas), *Danaus plexippus* (circumcontinental), *Vanessa cardui* (worldwide), *Nymphalis californica* (U.S. and Canada), *Libythea bachmannii* (U.S.), *L. carinenta* (Americas), *L. labdaca* (Africa), and the moths *Urania leilus* (Neotropics) and *U. fulgens* (Central America). It is perhaps of significance that these species belong to the Pieridae, Libytheidae, and Nymphalidae, a set of families that are evolutionarily inter-related (Shields, unpublished libytheid study.) Also, all, of course, are common to very common species, and many are known to be strong, fast fliers with two or more broods and comparatively rapid generation time. One migrant female *Vanessa cardui* produced 685 larvae in captivity (Schrader, 1928).

It is known that *Ascia monuste* has a dark form (*phileta*) that is the migratory phase (Klots, 1951). I have noticed that *Vanessa cardui* migrants are larger with brighter colors than the non-migrant phase, generally. A parallel might be drawn here with Uvarov's phase theory of locusts, with solitary and migratory phases of the same species differing in morphology, coloration, physiology, and behavior (Poulton, 1929; Williams, 1957).

START OF A MIGRATION

Despite innumerable reports of butterfly migrations in progress, rarely have observations of their actual commencement been recorded. The circumstances surrounding the start of the flight are expected to shed the most light on the illusive cause of butterfly migration and perhaps the origin of the navigation of the flight as well. Accordingly, the details of published accounts of the start of migration that I have been able to locate are given in full.

Sir Guy Marshall recorded that the migration of *Catopsilia florella* was actually taking place from a Rhodesian valley (Poulton, 1931).

Pitman (1928) gives an account of the crowded breeding-grounds of *Belenois mesentina* in the West Nile Province of Uganda, from which start the great southward migrations in Uganda and Kenya. In a grassy plain some 2 miles broad and 7-10 miles in length their foodplant (*Maerua oblongifolia,* Capparidaceae) was abundant "in full, tender leaf and flower," in March 1928 following a few heavy thunder-showers after which the weather continued exceptionally hot and dry. The area had evidently been burned out some weeks previously. Most of the foodplants were leafless; "larvae and chrysalises were to be seen everywhere, as also countless thousands *in cop.*" soon after emergence. "I have never before seen such countless myriads of butterflies, and as far as the eye could see there was a shimmer of white just above the surface of the ground." Preceding this emergence the West Nile was in drought for nearly twelve months. The adults were of small size, evidently due to starvation from the over-population. No actual migration of the adults, however, was observed.

Heape (1931, pp. 148-150) records a migration of *Catopsilia* (?) in the states of Ceará and Piauhy, Brazil, the end of January or early February, 1915, after the rains had started, from the mangrove swamps on the right bank of the River Camocim; "the flight was somewhere to the north of west." 36 hours after the flight began, it was followed on horseback by two men for 4½ days and 125 miles. "They diminished markedly in numbers the further westward they travelled." By the time the town of Sao Pedro was reached, some 50 miles further, the flight had ceased ("petered out"). One observer returned to Camocim and learned "there that the flight continued to emerge from the mangrove swamp for forty-eight hours after he had left the place, and then a heavy storm put an end to those which still remained in the swamps and the flight stopped."

"It is of particular interest to note that the route followed by these gentlemen passed over the high ground east of the Paranahyba River, and from there on to Sao Pedro, through sandy hills and rocky flats where the scrub was dried up, although it was the rainy season; and all over this country large numbers of the butterflies were seen lying dead. They most certainly had not laid eggs there, and it was judged they fell from exhaustion while *en route,* leaving a trail of dead bodies."

Collenette (1928) witnessed the start of a migration of *Libythea carinenta.* Between Corumbá and Urucum, Matto Grosso, Brazil, November 1927, "extraordinary numbers" covered muddy areas in the road all day long from November 16-21. November 22-23 was rainy and cool, with the mud practically deserted. Then on November 24, a bright and clear day, the migration started, many flying S and SSE starting about 7:30 am, while large assemblages were still on the mud. "At one such mud gathering, two or three in a minute rose and joined the passing stream, taking the general direction at once, without hesitation. In the instances which I was able to watch closely, there seemed to be no preliminary fluttering or walking about before taking to wing, and those which rose did not chase or play with those already in flight." None of the passing migrants were seen to settle on the mud, though they "frequently paused and fluttered over the gathering." He noted only three or four instances of pairing. At 9:45 am he left for Corumbá in the direction from which the *carinenta* were coming "in much the same numbers." "The insects quickly became fewer, and in about a mile I reached the drier vegetation, in which practically none were present, and where no migration was visible." He believed the swarm had "bred locally or had been attracted from the drier country in the neighbourhood."

Skertchly (1879) discovered the pupae of *Vanessa cardui* very numerous on grass blades between the mountains and desert in March 1869 west of Sowakin in the Sudan of Africa, soon after daybreak. "Presently the pupae began to burst, and the red fluid that escaped sprinkled the ground like a rain of blood. Myriads of butterflies limp and helpless crawled about. Presently the sun shone forth, and the insects began to dry their wings; and about half-an-hour after the birth of the first, the whole swarm rose as a dense cloud and flew away eastwards towards the sea. I do not know how long the swarm was, but it was certainly more than a mile, and its breadth exceeded a quarter of a mile."

Abbott (1951) records that John Garth found *Vanessa cardui* perhaps near the start of a migration at Santa Maria Bay, Baja California, 600 miles SSE of San Diego. "Thousands" of adults were seen, many of them emerging. Many flew south a short distance to the edge of the cliff, then north again to the breeding area, but no migration as such was in progress. It is probably significant that they were observed in a migration year, and at about the same dates as in California.

Emmel and Wobus (1966) noted *Vanessa cardui* near Florissant, Colorado in large densities (but no mass movement) from mid-July to mid-August, 1965. Then on August 22nd they "began flying about due south and south-southwest in vast numbers, and this mass movement, involving every individual seen, continued until August 25. By this date, almost all *V. cardui* had left this area but scattered individuals were observed flying south through August 28, when a cold front moved in and stopped all butterfly activity for several days." The flight started at 7:00 am to nearly dusk. Between September 1-19, *V. cardui* continued moving southward in reduced numbers. On September 20th a severe cold front moved in, apparently curtailing the migration.

END OF A FLIGHT

Williams (1930, p. 353) says migrants "frequently pass over large areas of land apparently entirely suitable for their inhabitation, but continue on and on as long as the migration hysteria lasts, and may end up in the open sea or in entirely inhospitable lands where breeding is impossible." "There are records of swarms of butterflies reaching the coast and flying steadily on out to sea" (p. 389). At Arolla, Switzerland, August 6, 1903, *V. cardui* in large numbers of big faded specimens "invaded the district and settled down, each on its own piece of land, to alternate duties of fighting with a neighbour and egg-laying" (Williams, 1930).

LACK OF RETURN FLIGHTS

It seems a paradox that migrations of *V. cardui* and others are unidirectional and nearly constant when they occur, yet return flights to replentish the migrant gene pool appear rare or non-existent. If accurate, somehow the species is repetitive in behavior in migration years (a mass exodus serving as a "safety valve" on the population). Thus perhaps most but not *all* of the migrant population departs during years of migration.

EFFECTS OF OVERCROWDING

According to Poulton (1902), "The [migration] instinct . . . compels the individuals to move together in vast masses in the same direction, rather than to scatter and fly in all directions." "The sugegstion is made that the crowded masses, resulting from over-production and inability of enemies to cope with the increase, are injurious to the species, because it is likely that food-plants would be checked for years or even killed out altogether in certain localities, while the heaps of dead individuals would encourage the attack and rapid spread of bacterial foes." The advantages derived from removal of the surplus from an overcrowded area would account for the development by natural selection of the instinct to move. Otherwise, there would be a destruction of the species in the area of overproduction.

Poulton (1921) quotes Trimen as saying, "The instinct to emigrate probably exists in a dormant state in all species liable to outrun the food-supply in any part of their range." If the overcrowding is unchecked, it would threaten the existence of the foodplant over a wide area. Near Mombasa, Africa, *Libythea laius* and other butterflies "appear only in occasional years . . . after a period of prolonged and severe drought," [when parasites, diseases, predators at a low, vegetation lush, and numbers would thus build quickly.] In some cases the migrant has stripped the leaves and shoots of its foodplant, such as *Catopsilia florella* on *Cassia arachoides* in Griqualand West in 1881.

Heape (1931) says, "All the evidence I have gleaned from investigation of the voluntary movements of the higher animals points, to my mind, definitely to the conclusion that emigration [of butterflies] is induced by overcrowding and the scarcity of food" (p. 158.) "Whatever may be the cause of these mass movements the result is that thereby huge surplus populations are effectually disposed of and the world saved from the incalculable devastation they would cause if they lived" (p. 171). "I have already suggested that the access of virility which attends the growth of the gonads and the development of reproductive cells in the higher animals, may well be the exciting cause of that stimulus which urges towards adventure of such kind [migration]; and that the resulting condition of a horde of individuals so affected my attain to what we call hysteria. I further suggest that, in spite of the radical differences both in the sense organs and in the central nervous system of insects, a condition comparable to hysteria may similarly be induced in them" (p. 170). "These conditions [i.e., the periodicity of migrations] are probably of climatic origin and affect the quality of the food supply and so govern reproductive activity."

In observations of migrating Lepidoptera often the "genital products" are in a backward condition (i.e., immature), and a migratory flight is necessary for their full development. Thus the stimulus to migrate may be a physiological one (Poulton, 1929).

Chapman (1939) mentions that Gause talks of "relaxation oscillations" arising from a relaxation or a decrease of environmental resistance, followed by a sudden population increase causing outbreaks. In insects having a high biotic potential, this relaxation during a single generation may result in a population increase of outbreak proportions.

Alexander (1961, fig. 63) suggests that field crickets under high density, crowded conditions showed no male territoriality and dispersed widely, compared with individuals in isolation which developed male territoriality and dispersed little.

It should be mentioned that *Colias eurytheme* often forms dense swarms numbering as much as some migrations of other species, but is not known to migrate unidirectionally (F. T. Thorne, pers. comm.).

INHIBITION OF STIMULI

Kennedy (1961) thinks "Migrants are distinguished by a transient accentuation of locomotor functions with depression of vegetative functions, such that the insect now travels." "The Nielsens listed the reflex patterns of adult *Ascia monuste* 'living in a territory' as feeding, mating, egg-laying, basking and cleaning, and reported failure to respond to the appropriate stimuli for any of these when the butterflies were engaged in unidirectional flight elsewhere." "Ecologically, migration sometimes looks like an alternative to diapause when conditions will no longer permit growth, development or reproduction." "The internal inhibition of certain reflexes is the behavioural component of a whole physiological syndrome."

POST-TENERAL EXODUS FLIGHT

According to Johnson (1960), "Whenever the start of a 'mass migration' of insects has been described—and this is very rare in spite of a voluminous literature—the insects have always been making either their first flight as new adults or one very soon afterwards." He makes reference here to *Catopsilia crocale*, *C. pyranthe*, *Ascia monuste*, *Vanessa cardui*, and *Nymphalis californica* doing so, from the breeding site. There was only ca. 1 hour between emergence and migration in two instances of *Vanessa cardui*. "The initial orientation of the insect in flight is probably 'imprinted' during the teneral period, or determined at take-off." "Too long an enforced wait before take-off, leading to sexual maturation or fertilization, apparently inhibits migration altogether in *A. monuste*."

OVIPOSITION

In *Catopsilia pyranthe* in Ceylon, "every female seemed possessed with the one insane idea of getting rid of her eggs with the utmost expedition . . . and then madly continuing her flight" (Poulton, 1921). *Belenois mesentina* females in a migration at Peradeniya, Ceylon, were often seen "to stop and lay eggs on bushes of *Capparis pedunculosa,* rejoining the migratory flight as soon as a few eggs had been laid" (Poulton, 1929).

SEX RATIO

Williams (1930, p. 344) says males mostly predominate in pierid migrations checked (24 cases), while females predominated in two instances (of *Catopsilia*). In five instances of *V. cardui,* females predominated (Europe), while in two instances males predominated (p. 345). A migration of *Catopsilia pyranthe* and *C. pomona* in Ceylon in November 1905 had the main flight 87% males, but later stragglers were almost entirely females (p. 346). (Males generally emerge first before females in butterflies.)

PARALLEL BETWEEN MAMMAL AND BUTTERFLY MIGRATIONS

Deevey (1960) delves into cause of lemming migrations; they are neurotically sick during migration. The "shock disease" causes them to die in numbers "from their own excitement." Food, predators, disease, and weather periodically relax a hold on lemming numbers. It is the younger lemmings that migrate. Also, the end result is a wipe-out (population crash) of migrating individuals largely, in lemmings (and certain insect migrations). When there are large numbers of rats, these display a "pathological togetherness" (i.e., prefer to live together, low fertility, shortened lives). In mammals, Christian (1950) reported that there is a sudden die-off in late winter and early spring following a population peak, due to the exhaustion of the adreno-pituitary system ("shock disease"). "The terminating factor is the attainment of a population above the carrying capacity of the environment." The population is under highly stressed conditions and taxes the adreno-pituitary system to the maximum.

Direct experimental evidence that butterfly migrations undergo a similar "shock disease" is lacking. However, there is observational evidence that this syndrome does in fact take place. Bernheim (1917) records a massive *Libythea bachmannii* migration near Eagle Pass, Texas, September 4, 1916. "There were literally millions of them and many of them had evidently completed their alotted span of life as they were dropping from the air in large numbers. One particular specimen flew past, almost brushing my face, and, as I thought, alighted upon the ground. As I stooped to examine it the wings suddenly folded down tightly in front of the body and I picked the insect up quite dead." Heape (1931, pp. 148-150) reported large numbers of a *Catopsilia* (?) sp. lying dead after its migration through the territory, in Brazil. On April 15-20, 1973, I noticed fresh *Vanessa cardui* bodies forming windrows along the hiway during a migration in the Eastern Mojave. Some appeared to fall dead to the pavement from the flight merely from the wind of passing cars. Hayward (1953) says that on December 26, 1951, there was an *Ascia monuste* migration in Argentina present in the millions, with thousands of dead on the ground, many in fresh condition.

POSSIBLE CORRELATION WITH SUN-SPOTS

Grant (1937) has noted a correspondence in years of outbreak (40 out of 60) in *Celerio lineata* moth migrations in Europe and North America. "In seeking for an explanation of the outbreaks of *l. livornica* and *l. lineata*, one must look for some large cause, wide enough in its effects to have influenced both continents simultaneously." She found some relationship between the outbreaks and 11-year sunspot cycles over a 100 year period (fig. 5). "The number of outbreaks would seem to rise from the minimum towards the maximum, and then fall away towards the next minimum . . . ," with some exceptions. She also found a strong tendency for outbreaks to occur when a wet year has followed a dry year. Williams (1965, p. 158) found a tendency for simultaneous abundance or rarity in North America and Europe in *V. cardui* from 1865-1938, statistically more significant than Grant's *Celerio lineata* correlations! Williams, however, said he could find no apparent correlation in *C. lineata* and *V. cardui* outbreaks to sun-spot cycles. With *V. cardui* there were above average numbers at both the maximum and minimum sun-spots, with below-average numbers on rising and on falling periods in the cycle.

Brown (1974) mentions there are recent suggestions of interrelationships between solar activity, the Earth's magnetic field, and the weather. Periods of maximum sun-spot activity show an 11-year cycle. Wood & Lovett (1974) found a highly positive correlation of drought years in Ethiopia and sunspot minima (from 1540 to 1974). Over a 72 year period there, "The rainfall clearly follows a cyclic pattern in which rainfall peaks and troughs precede the sunspot peaks and troughs by a few years" (i.e., to 2 years). "Thus, there is a strong statistical correlation between Addis Ababa rainfall and sunspot number, the rainfall peaks leading the sunspot peaks by an average of 1.3 yr." Thus there would indeed appear to be some correlation between *V. cardui* outbreaks and the sunspot cycle, i.e., occurring after several years following rainfall peaks and extreme droughts.

RAINFALL

Williams (1965, p. 23) says, "Painted Ladies breed during the winter along the edges of the great North African desert belt, and then move north in the spring across the rest of North Africa, the Mediterranean and Europe." In Ceylon, the NE monsoon starts in about October with very heavy rainfall. "This is followed immediately by great flights of butterflies," lasting for about 3 months, "and then, after a lull, there is a recrudescence of activity in March and April corresponding to the end of the north-east and the beginning of the south-west monsoons" (p. 53). At Portachuelo Pass, 3500′, Venezuela, Beebe noted 250 species of butterflies "migrating" through; "the flights seem to be associated with the rainy season, which lasts roughly from April to November" (p. 44).

WIND

Of 367 recorded observations of directional flight by butterflies in which the direction of flight and wind had been recorded, there were little or no significant differences in proportion among flights with the wind, diagonally with and against the wind, across the wind, and against the wind (Williams, 1949).

DIRECTION OF FLIGHT

Williams (1949) notes that in the tropics, flights of the same species tend to recur in the same direction at the same season in different years. "On reaching an obstacle most migratory butterflies pass *over* it rather than *round* it. . . ." "Migratory butterflies have also at times been observed to follow the windings of deep valleys, of roads through forest, and of shorelines. . . ." "There are . . . a few observations of simultaneous flights of two or more species, each flying in a different direction through the same locality for many days, and each keeping to their own direction." The movements of both such species had no apparent effect on the other. It is often noticed that butterfly migrations cease or are much reduced when the sun is clouded. "Orientation is quite definite at midday in the tropics when the sun is so near the zenith as to be practically useless for horizontal orientations" (Williams, 1957).

Flights of migrants that follow the shore line and do not fly out to sea, e.g., *Ascia monuste, Erynnis zarucco funeralis,* and *Urania fulgens,* suggest that topographic features play a part in determining the success of a migration, rather than it being a totally suicide flight.

Welling (1964) found *Calpodes ethlius* in Panama in its migrations "does not adhere to one single direction, mention being made of it 'passing in almost every direction' in the course of a single afternoon and evening." He saw one migration going N to S, slowly changing from W to E, then finally changing from SW to NE in one hour. They were therefore flying circles within that particular grassy swamp.

A *Catopsilia sennae* migration continued to fly during a tropical thunderstorm with heavy rain but oriented randomly (Johnson, 1969, p. 155). In a migration of *Catopsilia statira* in Trinidad, Williams noticed that when he attempted to catch examples, "any butterfly narrowly missed was put off its direction by the excitement and flew off wildly in any direction. Other butterflies close at hand meeting this butterfly flying out of the general order would in turn become confused and sometimes follow it in its new direction. So that after several misses in succession I was surrounded by a number of butterflies flying in all directions. If I stopped attempting to catch specimens these would gradually pass away, and the regular direction of flight would be resumed" (Poulton, 1921).

I reported (1967, p. 112) that migrations of *Vanessa cardui, Danaus plexippus,* and a *Delias* sp. are known to pass over summits of hills and mountains. No "staying" at the hilltop was shown by these. One migration of *V. cardui* on Dictionary Hill summit flew upslope from the south, flew across the summit, and instead of flying down the other side flew up and out off the north slope. Others were seen to pass over the hill's shoulders. No concentration toward the summit by the flight was noted. This could be a "breakdown in territoriality" (F. T. Thorne, pers. comm.), as resident *cardui* continued to "hilltop" that day. Wright (1906, p. 37) records a migration of *V. cardui* on top of "Grayback," 11,600′, that was going due east. They flew up the slope of the mountain and upon reaching the top, where the crest dropped off suddenly, "they kept straight on as far as the eye could follow them, right up into the sky. . . ." A *V. cardui* migration was seen flying over a 1300m summit in Austria in 1877 (Williams, 1930).

Tulloch (1912) reports an *Atella phalantha* migration on Mauritius, on the Trou-aux-Cerfs, an extinct volcano. Immense numbers flying up the crater towards the east; at the top they flew to the other side of the crater, then downhill to the bottom, where they went "right-handed round the base of the volcano" until they reached where he had been before, where they went uphill. "In fact, the butterflies were all going on an endless round, up the hill, across the top, down again, and round to where they started." The atmosphere was very clear, bright, and hot; a westerly breeze was blowing.

Abbott (1951) says *V. cardui* in southern California fly to the NW mostly, but also NNW or N. He says one would suppose butterflies following a definite compass direction would fly across a canyon from rim to rim, but instead *V. cardui* flies down one side and up the other, "keeping about the same distance from the ground all the time." "Butterflies which approached the lee side of a hill, flying NW, changed their course when they came to the top of the hill, turning and flying against the SSW wind. While they were turning, one single butterfly was seen to keep on toward the northwest." He notes that some upon encountering a wall in their path rose in the air in a "spiral" until clearing the roof, proceeding then NW.

NAVIGATION

Vleugel (1952) believes that the sun is the governing factor in the orientation of butterflies, based on bird migration studies. He supposes that somehow the "migrating butterflies allow for the change of angle necessitated by the apparent movement of the sun." However, Williams (1965, p. 126) defeats the argument for a sun-compass direction that allows for the angle change necessitated by the apparent movement of the sun: (1) the migrant would have to allow for the rising of the sun each morning at a 180° angle from sunset as flights resume each morning in the same direction as the previous evening, (2) when delayed for several consecutive days by bad weather they still resume their flight in the correct direction, and (3) they can migrate at mid-day in the tropics when the sun is overhead and therefore useless for direction finding. No known organ in insects seems likely to be sensitive to the Earth's magnetic field, according to Williams.

Perhaps a means of circumventing these difficulties is to assume that the freshly emerged migrant adults navigate by using polarized light at the time of day they would normally start exhibiting territoriality and "freezing" upon this angle (D. A. Watts, pers. comm.). This fixed polarization would overcome the problem of having to adjust to a changing sun angle throughout the day. *Vanessa cardui* spring migrations in northern Africa-Europe and in California both trend mainly NW (compare Williams, 1925, fig. 2 with Abbott, 1951, fig. 1), while in the southern hemisphere in SE Australia, *V. cardui kershawi* migrations fly predominantly S to SW during spring (August to November for some 7-8 weeks) (Smithers, 1969). *Vanessa* normally exhibits "hilltopping" and territorial behavior in the afternoon starting from 12:30-3:15 pm PST (Shields, 1967) but peaking in late afternoon, while feeding at flowers in the morning. The sun in the afternoon would be in the SW quadrant of the sky in the northern hemisphere (above the Tropic of Cancer) and in the NW quadrant in the southern hemisphere (below the Tropic of Capricorn) in the spring, so that the *V. cardui* migration direction would be "fleeing" at nearly right angles from the sun's incident light. This is along the direction of the plane of polarized light, as can be seen with a Polaroid sheet. I.e., in the morning in the northern hemisphere above the Tropic of Cancer, the plane of polarization rotates from N to E and S to W, while in the afternoon it rotates from W to N and E to S. For *Libythea bachmannii* the majority of the migration records are toward the E or SE in July-September (SE predominant) in Texas., and *Libythea labdaca* flies in March-May to the SW, SSW, S, SE, ESE in Nigeria and Gold Coast, with one record of *L. laius* in May in Tanganyika flying N (Williams, 1930). Here the *Libythea* would be using the plane of polarization to fly *toward* the sun. A summary of ca. 25 migrant species from Kodaikanal, S. India by Evershed (Williams, 1930, p. 297) showed primarily N-NE, S, SE movements in six species in February-March [sun slightly southward], northward and NE-E-SE movements in May-June [sun slightly north], and 100% southward movements of nearly all the species in August-November (primarily October) [sun southward to far southward]. Waterman (1955) says that light from the sun as transverse electromagnetic waves is partly polarized by the scattering of light by air molecules. To the human eye, this polarization is nearly invisible.

Mazokhin-Porshnyakov (1969) says that sunlight is polarized up to 70-80%. It is known that various aquatic crustaceans, the horseshoe crab, some terrestrial arachnids, and winged insects (certain Coleoptera, Hemiptera, Diptera, Hymenoptera, Trichoptera, and Lepidoptera) react to light polarization; both faceted eyes and simple ocelli are sensitive to polarized light. Honeybees can quickly learn to distinguish between two light beams polarized in different planes. Impulses within the optic lobes arose following a rapid 90° rotation of the polarized plane in honeybees. "According to Autrum and Frisch, the insect's ability to recognize different polarization planes is due to the radial distribution of the visual cells in the forms of a rosette. If we suppose that each visual cell is sensitive to polarized light in a given plane, then the whole rosette would act as a polarization analyzer." "Electron microscopy investigations of the rhabdom in insects and other arthropods . . . revealed that polarization analysis is a property related to the rhabdomeres' periodic ultrastructure which repeats itself in different ommatidia. . . . Organic molecules absorb light when it is polarized in the same direction as the longitudinal axis of the chromophore. Since the visual pigment molecules are regularly oriented within the rhabdomeres . . . and absorb more strongly when the light is polarized in preferred planes (dichroism), they could . . . act as a polarization analyzer" (p. 141).

Vowles (1950) noted that ants (*Cataglyphis, Monomorium, Myrmica*) maintained a constant angle of orientation relative to the plane of polarization of light, in experiments (field and lab). With *Myrmica,* by altering the plane of polarized light with a Polaroid sheet, a new angle was assumed by the ant to the dorsal beam of plane-polarized light (his graph), but not to one of ordinary light. A tortricid larva (*Archips cerasivorana*) that crawled toward the sun was induced to turn 90° by placing a polarizing sheet over it as it moved, with continued maintenance of the new course under the influence of the polarizing sheet (Wellington, 1955). "It is common to see both larvae and adults fall victims of heat stroke on a sheet of paper while they are engaged in ineffectual circling movements in response to rapid changes in the sky," due to clouds or smoke. ". . . the sun is primarily a heat source, and . . . the plane of polarization is the primary means of maintaining orientation to the sun . . . when an insect crosses an open space in daylight," according to his experiments. "The compound eye of an insect is fixed on the head and seems to be especially suitable for recognizing the polarization over the whole sky at once, providing that we assume that it can act as an analyzer of polarized light" (Frisch, 1950, pp. 90-96).

NIGHT MIGRATION?

Reports of butterflies migrating at night may be spurious unless actually observed to do so. The only migration claimed to be observed taking place at night that I am aware of is "Eagle Clark's observation . . . that . . . *V. cardui* flew toward England from the Continent against a wind *at night*" (Shannon, 1915, p. 618). Kendall & Glick (1972) record many instances of diurnal butterflies collected at visible and ultraviolet light at night, including some migrant species. "Evidence indicates most diurnals must be disturbed from their resting places before they appear at induced light" (p. 275). Thus, claims of butterflies migrating at night because they were taken at lights are probably unjustified. Their high density in the vicinity would account for some turning up at light. An exception would seem to be a report by Kingdon (1932) of a ship 87 mi. at sea with *Vanessa cardui* at lights at midnight thought to have come on board the previous hour. There was a strong off-shore wind, and had been all day. However, Williams (1930, p. 342) noted individuals of a swarm of *Pieris brassicae* resting on the surface of the ocean and taking flight when disturbed, so it is possible the *cardui* were roosting nearby on the water. Even large-scale migrations take place only from sunrise or somewhat later (start) until sunset or dusk (cease) (Williams, 1930; Hayward, 1953; Smith, 1972). Birds can use celestial navigation in their migrations (Wallraff, 1960) but butterflies do not appear to do so.

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